

SOME NEMIC PARASITES AND ASSOCIATES OF THE MOUNTAIN PINE BEETLE (*DENDROCTONUS MONTICOLAE*)¹

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INTRODUCTION

A study of the nemic parasites and associates of bark beetles is of both economic and scientific interest. Some of the new species proposed by Fuchs^{3 4} in his recent works on the nemic fauna of the bark beetles of central Europe must be considered detrimental to the beetles and therefore of economic importance. The limited observations recorded in the present paper indicate that the nemic fauna of all bark beetles known to occur in the United States should be investigated, as some of the nemas may prove of value in the control of the beetles by acting as disease carriers and as consumers of weak or even healthy beetles and their eggs.

Closely related to the determination of economic importance is the study of the ecological relations existing between the nemas and the beetles. Of special interest also is the classification of the various genera and species. Both of these latter aspects of the subject are discussed in the present paper.

MATERIAL

The material used in the present investigation was collected at Metaline Falls, Wash., in July and August, 1930. Some of it was taken from under the bark of a pine that had been killed by the mountain pine beetle (*Dendroctonus monticolae* Hopk.) in 1929 and some from a pine that had become infested not more than 10 days before the date of collection, July 18, 1930.

ECOLOGY

RELATION OF NEMAS TO BARK BEETLES

Some of the new nemic genera proposed by Fuchs⁵ are extremely close to free-living genera, and the various species represent almost every intermediate stage, thus illustrating the manner in which parasitic nemas may arise from free-living forms. From a mere occurrence of the nemas in the mines of the bark beetles and their possibly accidental use of the beetles as carriers, the way to true parasitism seems to proceed by the following steps: (1) The use of the bark beetle as unconditional carrier, (2) the extension of the carrier association into a regular life association under the wing covers or on

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² The material for this investigation was collected by D. DeLeon, formerly of the forest insect field station, Bureau of Entomology, U. S. Department of Agriculture, at Coeur D'Alene, Idaho.

³ FUCHS, G. DIE NATURGESCHICHTE DER NEMATODEN UND EINIGER ANDERER PARASITEN. 1. DES IPS TYPOGRAPHUS L. 2. DES HYLOBIUS ABIETIS L. Zool. Jahrb., Abt. System., Geogr. u. Biol. Tiere 38 : [109]-222, illus. 1915.

⁴ ——— NEUE AN BORKEN UND RÜSSELKÄFER GEBUNDENE NEMATODEN, HALBPASARITISCHE UND WOHNUNGSEINMIETER. FREILEBENDE NEMATODEN AUS MOOS UND WALDERDE IN BORKEN-UND RÜSSELKÄFERGÄNGEN. Zool. Jahrb., Abt. System., Ökol. u. Geogr. Tiere 59 : [505]-646, illus. 1930.

⁵ FUCHS, G. Op. cit. (See footnote 3.)

the exterior surface of the beetle, (3) the production of special cocoons and webs by the nemas on the body of the beetle, (4) the habit of feeding on the beetle itself from the outside (ectoparasitism), and (5) true endoparasitism of the nemic larvae.

ECOLOGICAL GROUPS OF APHELENCHOIDES

Certain species of *Aphelenchoides*⁶ are free-living; others are parasitic, either on plants or animals; and there are numerous intermediate species. Fuchs separates his *Parasitaphelenchus* into the three following ecological groups:

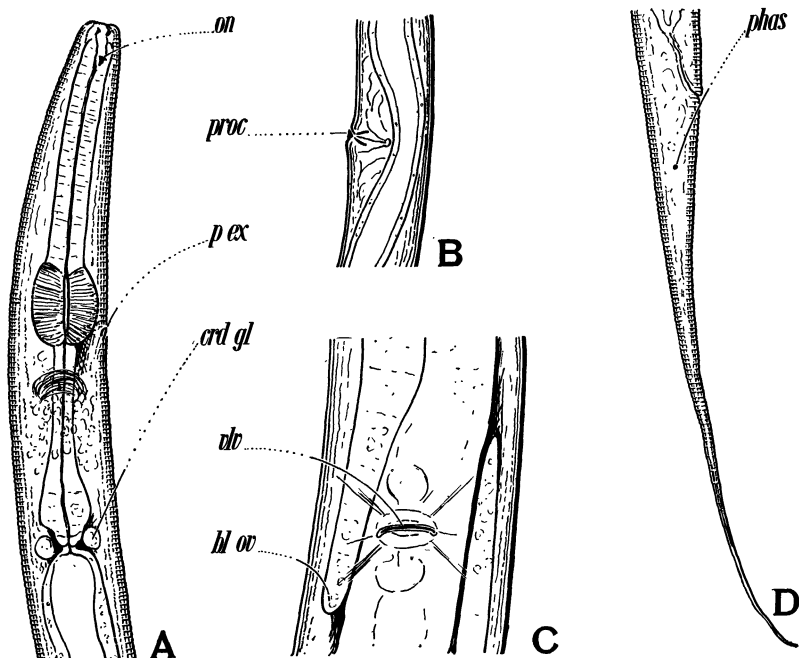


FIGURE 1.—*Diplogaster occidentalis* (female). A.—Head end in lateral view: *on*, onchium; *p ex*, excretory pore; *crd gl*, cardiac gland. \times about 750. B.—Vulvar region in lateral view: *proc*, toothlike process. \times about 530. C.—Vulvar region in ventral view: *vlv*, vulva; *bl ov*, blind end of anterior ovary. \times about 1,090. D.—Tail: *phas*, phasmid. \times about 530

(1) Species whose larvae live as parasites in the body cavity of bark beetles. (Endoparasites.)

(2) Species whose larvae are found with or without a cocoon either under the wing covers of bark beetles or attached sucking on the backs of the beetles. (Ectoparasites.)

(3) Species whose larvae and adults are found in the frass of the mines or on the beetles themselves, but under conditions not indicative of true parasitism. (Free-living.)

This classification outlines the three main aspects of the relationship between the species of *Aphelenchoides* and the bark beetles. The two species described in a later section of the present paper, from the mountain pine beetle of Washington, apparently represent true endoparasites. Only adults were seen, but it is highly probable that the larvae develop within the body cavity of the beetles. A still more pronounced type of parasitism is possible—that in which not only the larvae but also the adults are endoparasites. That this type of

⁶ Synonyms: *Pathoaphelenchus* Cobb, and *Parasitaphelenchus* Fuchs. (See footnotes 4 and 10.)

parasitism occurs in the genus *Aphelenchoides* is not known, but it may be considered possible in view of the present meager knowledge of these forms.

A number of other genera described by Fuchs⁷ from various bark beetles show a trend toward parasitic life, but the process is especially impressive in *Aphelenchoides* because the most closely related forms, such as species of *Aphelenchus*, *Paraphelenchus*, and *Schistonchus*, are well-known free-living or plant-parasitic species. A somewhat new conception of the status of these genera is suggested in the present paper.

DIPLOGASTER AND THE MOUNTAIN PINE BEETLE

Tendencies toward parasitism are evident in the genus *Diplogaster*, although at present there is no species known that may properly be called a parasite. The species described herein is considered by the writer to be an associate, rather than a parasite, of the mountain pine beetle. These nemas inhabit the mines and frass and are probably carried by the beetles from one mine, tree, or locality to another.

TAXONOMY

DIPLOGASTER OCCIDENTALIS, N. SP.

Diplogaster occidentalis (figs. 1-3) is closely related to a group of forms, namely, *D. rhodani* Stefanski, *D. nudicapitatus* Steiner, *D. lineatus* Fuchs, and *D. consobrinus* De Man.⁸ Of these four forms, only *D. lineatus* is described from bark beetles. It was found in the mines of *Hyllobius abietis* L. from Europe. *D. occidentalis* is also found living in bark-beetle mines. In all, 175 specimens were observed, including 47 males, 92 females, and 36 larvae.

The largest males are about one and one-half times as large as the smallest. Males, females, and larval specimens have an elongated filiform tail; in the male the base is somewhat set off from the slender end portion. (Fig. 3, C.) The cuticle has 18 equidistant uninterrupted longitudinal wings of the same height. (Fig. 3, B.) The intermediate portions of the cuticle, however, show annulation. A cross section shows the lateral and ventral cords to be rather wide (fig. 3, B); no dorsal cord was seen. The head structures are somewhat obscure. There seem to be six lips, each having a papilla. (Fig. 2, A.) In a front view, small slits just behind the lateral papillae are interpreted as being the external amphids. The oral opening is triangular in shape, with the three corners well cuticularized and distinct. The form of the pharynx is rather indistinct; its walls are not well cuticularized and are only partly thickened (fig. 2, B); it is narrow but deep, and of somewhat irregular shape. What appears to be an onchium is situated at its base; for an onchium, however, it is little cuticularized. The anterior cylindrical portion of the esophagus is followed by a well-developed medial bulb, which exhibits numerous radial muscle fibers and long but thin valvulae. The isthmus and terminal bulb are typically diplogastroid, clear and rather transparent. Three cardiac glands were seen. The excretory pore opens ventrad of the middle bulb. The female apparatus is amphidelphic, with the reflexed ovaries extending back to the vulva or even past it. (Fig. 1, C.) The transparent vulva is slitlike (fig. 1, C); its posterior lip, in profile view, seems to form a toothlike process (fig. 1, B). The male has a single reflexed testis. (Fig. 3, A.)

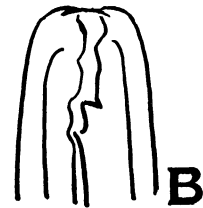
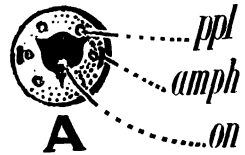


FIGURE 2.—*Diplogaster occidentalis*. A.—Front view of head: ppl, papilla; amph, amphid; on, onchium. \times about 1,610. B.—Free-hand sketch of pharynx

⁷ FUCHS, G. Op. cit. (See footnote 4.)

⁸ MAN, J. G. DE. DESCRIPTION D'UNE ESPÈCE DU GENRE DIPLOGASTER MAX SCHULTZE: DIPLOGASTER CONSOBRINUS NOV. SP. ANN. Soc. Roy. Zool. Malacol. Belg. 51: 47-54, illus. 1920.

Its copulatory apparatus is remarkable because of the large-sized gubernaculum—nearly as long as the spicula—especially well seen in side view. Linear distally, it widens considerably toward its inner end, which forms a rather wide plate ending with straight transverse truncation. The spicula are much finer; their proximal ends distinctly capitate. Distally the gubernaculum exhibits in side view a larger and, proximad to it, a smaller process; the ventral view, however, shows only the larger process, which then appears very prominent. (Fig. 3, C.) The protrusile muscle of the gubernaculum is remarkably strong; oblique copulatory muscles occur in front of the anus. The arrangement of the male copulatory papillae is shown in Figure 3, C and D. Of special interest are the

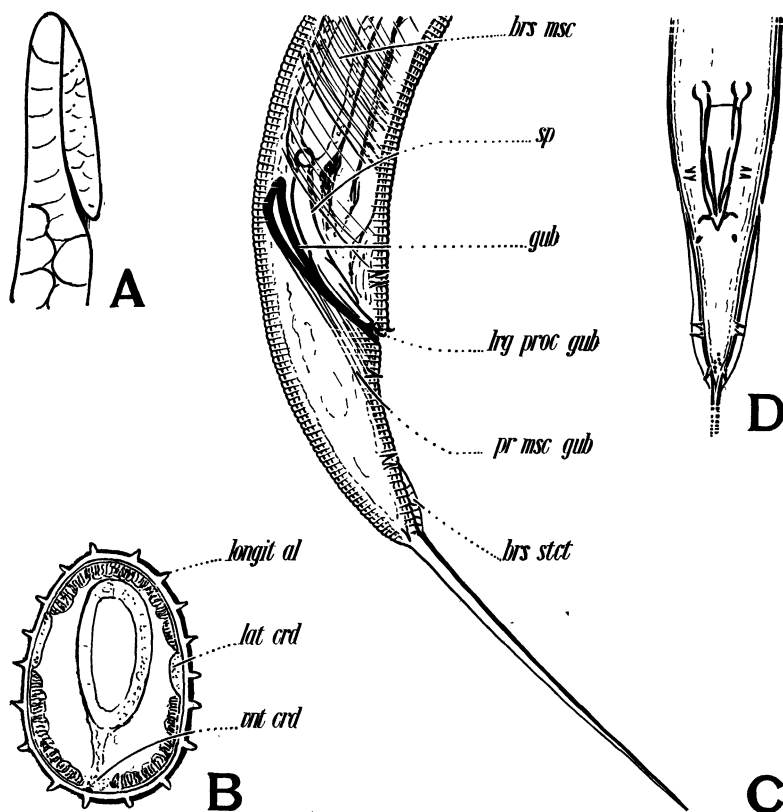


FIGURE 3.—*Diplogaster occidentalis* (male). A.—End of testis (free-hand sketch). B.—Cross section in middle region of body anterior to testis: *longit al*, longitudinal wing; *lat crd*, lateral cord; *vnt crd*, ventral cord. \times about 1,070. C.—Tail end: *brs msc*, bursal muscles; *sp*, spicula; *gub*, gubernaculum; *lrg proc gub*, larger process of the gubernaculum; *pr msc gub*, protrusile muscle of the gubernaculum; *brs stct*, bursalike structure. \times about 1,070. D.—Anal region in ventral view. \times about 665

small winglike or bursalike formations on each side of the tail of the male. (Fig. 3, D.) One of the papillalike lateral structures apparently connected with this wing may be a phasmid, which is clearly seen on the female tail. (Fig. 1, D.)

MEASUREMENTS:

Male:	1.1	13.0	19.0	'M	81.0	0.60 mm.
	1.9	4.5	4.8	5.6	3.7	
Male:	1.1	13.0	19.0	'M	80.0	0.43 mm.
	1.5	3.9	3.9	3.9	3.2	
Female:	0.7	13.0	17.0	'48.'	76.0	0.64 mm.
	1.3	3.0	3.5	4.1	2.8	
Female:	0.72	14.0	18.0	'46.'	75.0	0.625 mm.
	1.40	3.6	3.6	4.2	2.2	

DIAGNOSIS.—Diplogaster with 18 equidistant longitudinal wings, with distinct annulation in the interspaces. Head with six lips, each of which has a single papilla. Pharynx narrow, irregular, much longer than wide, without distinct separation into wider anterior and a narrow posterior portion, and with an indistinct, little cuticularized dorsal onchium at its base. Middle esophageal bulb with long but thin valvulae. Female apparatus amphidelphic, ovaries reflexed, ending past the vulva; posterior vulvar lip in profile view with small toothlike structure. Male and female tail long, conical at base, filiform at end portion. Male with a very prominent gubernaculum, at least five-sixths of the length of the spicula; copulatory papillae as shown in Figure 3, C and D.

THE GENUS APHELENCHOIDES

STATUS OF THE GENUS

Two species from the material used in the present study were found to be very closely related to a number of species recently described by Fuchs⁹ under the generic name of *Parasitaphelenchus*. Unfortunately Fuchs failed to give a generic diagnosis. His description reveals no characters that apply to all his species or differentiate them from other genera such as *Aphelenchoides*. All his species and also the two new species described in the present paper may properly be placed in the latter genus. The generic name *Aphelenchoides* is here used in the sense suggested by Cobb for *Pathoaphelelenchus*¹⁰ (which is antedated by the name *Aphelenchoides*¹¹). Its characters, which are here repeated, are those of the former genus *Aphelenchus*, but not those that must be recognized since the discovery of the males of the type species of *Aphelenchus*, *A. avenae*. This species exhibits characters that separate it widely from the forms with which it has hitherto been associated and which must now be included in the genus *Aphelenchoides*. The writer^{12 13} has given a fuller discussion of this question elsewhere.

Fuchs¹⁴ mentions for four of his *Parasitaphelenchus* species a character which, if proved to be valid, would fully justify the creation of a new genus, namely, the location of the nerve ring in front of the esophageal bulb in the species *Parasitaphelenchus typographi*, *P. dubius*, *P. conjunctus*, and *P. hylastophilus*. This position of the nerve ring, if established, is exceedingly remarkable, so much so that further observations must be made before it can be accepted. If, however, it is accepted as a generic character, most of the species included by Fuchs in the genus *Parasitaphelenchus* would have to be excluded.

At present, therefore, it is not possible to recognize *Parasitaphelenchus* as a genus in good standing, but it should be synonymized with *Aphelenchoides*. If a division of the latter genus is to be made, it could only be on characters that are not yet entirely clear and certain. If the future should show the need for the creation of a new genus, its characters will have to be formulated anew.

⁹ FUCHS, G. Op. cit. (See footnote 4.)

¹⁰ COBB, N. A. [APHELENCHUS RETUSUS WITH A PROPOSED DIVISION OF APHELENCHUS.] *Helminthol. Soc. Wash. Proc., Jour. Parasitol.* 14: 57. 1927.

¹¹ FISCHER, M. ÜBER EINE CLEMATIS-KRANKHEIT. *Ber. Physiol. Lab. Landw. Inst. Halle 3* (Heft 11): 1-11, illus. 1894.

¹² STEINER, G. ON THE STATUS OF THE NEMIC GENERA APHELENCHUS BASTIAN, PATHOAPHELENCHUS COBB, PARAPHELENCHUS MICOLETZKY, PARASITAPHELENCHUS FUCHS, ISONCHUS COBB AND SEINURA FUCHS. *Jour. Wash. Acad. Sci.* 21: 468-475, illus. 1931.

¹³ ANNOTATIONS ON THE NOMENCLATURE OF SOME PLANT PARASITIC NEMATODES. *Jour. Wash. Acad. Sci.* (In press.)

¹⁴ FUCHS, G. Op. cit. (See footnote 4.)

The generic characters of *Aphelenchoides* are as follows:

(1) The males have no bursa but only copulatory papillae; the spicula are short, strongly arcuate, proximally wide to very wide, distally more or less pointed; the gubernacula are absent; the testis is single.

(2) The postbulbar portion of the esophagus is more or less distinctly assimilated by the intestine, which therefore appears to begin immediately behind the esophageal bulb. This latter is the homologue of the middle esophageal bulb in *Tylenchus* and other genera.

(3) The outlets of the three salivary (esophageal) glands are located in the esophageal bulb, the dorsal one anterior and the two ventro-submedial ones posterior to the valvulae.

(4) The females are prodelphic with a more or less reduced posterior gonadic branch still present.

APHELENCHOIDES CONURUS, N. SP.

Only two specimens of *Aphelenchoides conurus* (fig. 4) were seen, and unfortunately one of them was lost during preparation. The following description is therefore based mainly upon a single female.

The tail is elongate-conical, but, in contrast to other species, not mucronate. The cuticle is annulated but has no wings. The specimen observed had a distinct lip region which exhibited all the characters typical of the genus. There are four submedial papillae, and laterally rather distinct amphidial openings. The spear is short but rather wide; notable is the absence of knots or swellings at its proximal end. The spear thus offers the best specific characters. The esophageal bulb is exceptionally large (fig. 4, A); its valvulae are distinct but not prominent; radial muscle fibers were not seen. The ampullae and outlets of the salivary or esophageal glands could be distinguished; they seem to have the normal position, that is, the position typical for *Aphelenchoides*. The dorsal gland opens in the anterior portion of the bulb and the two subventral ones in the posterior. The intestine begins at the bulb as a cylindrical tube which, however, swells after it has passed through the nerve ring. Its lumen is very indistinct; its tissue is filled with reserve material, the cell walls being therefore obscure. The rectum, too, is rather indistinct, perhaps not even

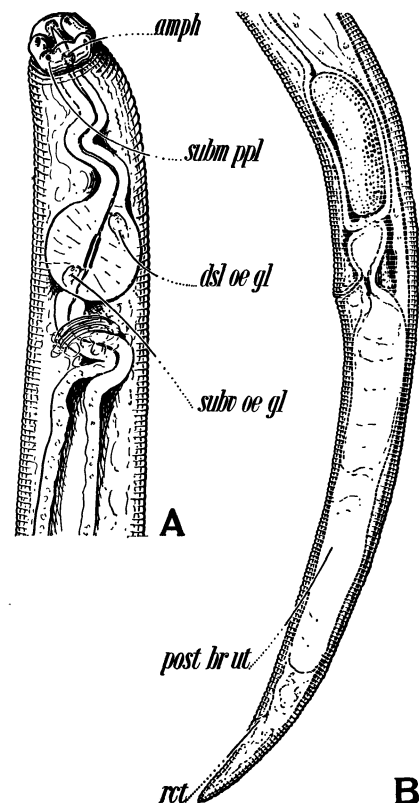


FIGURE 4.—Parts of *Aphelenchoides conurus*. A.—Head end of female: *amph*, amphid; *subm ppl*, submedial papilla; *dsl oe gl*, outlet of dorsal esophageal gland; *subv oe gl*, outlet of subventral esophageal gland. \times about 530. B.—Posterior portion of female: *post br ut*, posterior branch of uterus; *rect*, indistinct rectum. \times about 360

functional. The excretory pore was not seen. The female apparatus is prodelphic, but, as in other members of the genus, a large posterior branch of the uterus extends nearly to the anus. The vagina leads slightly forward. The eggs are about three times as long as wide.

MEASUREMENTS:

	0.8	6.3	7.0	80.0	96.3	
Female:	1.1	2.3	2.4	2.8	1.3	1.0 mm.

DIAGNOSIS—*Aphelenchoides* with elongated, conical nonmucronate tail. Spear short but wide, without basal swellings. Esophageal bulb large, spherical, apparently without radial fibers. Living as parasite and associate of the mountain pine beetle.

APHELENCHOIDES ACROPOSTHION, N. SP.

Several females and males of *Aphelenchoides acroposthion* were found. Compared with other members of the genus, this species is a very large form.

Although the specimens had the appearance of true parasites, no exact facts were known as to their relationship to the mountain pine beetle except that they have been found in the mines of the beetles. Since only adult specimens were present, one is led to suppose that their larvae may be endoparasites of the beetle.

The body is very slender and elongate. The tail of the female is short and bluntly rounded (fig. 5, A); that of the male is also short, and its base is similar to that of the female but with the difference that it ends in a short hornlike process (fig. 5, D). The cuticle is finely annulated, but no lateral membrane was seen. The distinctly set-off lip region exhibits in a front view six rounded, well-separated lips. (Fig. 5, B.) A cuticularized ring with six short rays encircles the oral opening. The structures of the head end were rather obscure, but it is believed that the amphids were seen in the position shown in Figure 5, B. This species, like other members of the genus, has four submedial papillae. The spear is extremely fine (fig. 5, E) and appears to be composed of three different portions—an anterior conical portion rather well cuticularized, a succeeding short cylindrical portion also well cuticularized, and then a long cylindrical portion which is hardly cuticularized and which, posteriorly, is set off from the esophageal canal only by the attachment of the protruding spear muscles. No basal swellings were seen. The esophageal bulb is well developed and of oval shape; it has rather long but thin valvulae. (Fig. 5, F.) The radial muscles attached to the valvulae exclude a more glandular portion at the anterior and posterior ends of the bulb. The connection of the intestine with this bulb is much the same as in other forms of *Aphelenchoides*. The nerve ring occurs a short distance behind the bulb. The intestine is of somewhat degenerate character; its cell walls can hardly be recognized, the whole organ being filled with reserve material. As in the previous species, the rectum and anal opening are extremely fine and obscure. No excretory pore was seen. The vulvar opening is well marked because the body narrows just behind it. The female sexual apparatus is prodelphic; there is, however, a well-developed posterior branch of the uterus, and attached to it there appears to be a vestigial ovary extending nearly to the anus. The anterior ovary extends forward nearly to the nerve ring. The very short sexual apparatus of the male is of the proorchid type, with the end of the testis reflexed. Figure 5, D, gives a lateral view, and Figure 5, C, a ventral view of the copulatory apparatus. It seems that the two spicula are amalgamated, forming a single spiculum, pointed at the outer end, but very wide at the inner end. The ventral apophysis exhibits at its inner end a short process pointing ventrad; the dorsal apophysis is somewhat swollen proximally. Only one male was studied in ventral view; it showed in the anal region a peculiar lateral expansion somewhat resembling a vestigial bursa. Two papillae were distinctly seen on the inside of this expansion, one in the anal region and the other at the base of the hornlike process. It is doubtful whether these males are fully functional.

MEASUREMENTS:

	0.8	5.7	6.2	M	99.2	
Male:		0.9	0.9	1.6	0.6	1.6 mm.
	0.5	3.5	4.1	78	82.3	16
Female:	0.4	0.8	0.8		92.0	99.0
					1.2	0.9
						2.4 mm.

DIAGNOSIS.—*Aphelenchoides* of long, slender shape. Tail of female short, obtusely rounded; that of male broadly conical at the base, mucronate. Spear rather narrow, of average length, without basal swellings. Esophageal bulb ovoid. Vulva well marked because the body narrows abruptly behind it. Male with slightly sublateral papilla in latitude of the anus, and another somewhat in front of terminal process.

SUMMARY

Some nemec associates and parasites of the mountain pine beetle are described and their economic significance is discussed. The various phases of the mutual relationship of the bark beetle and the

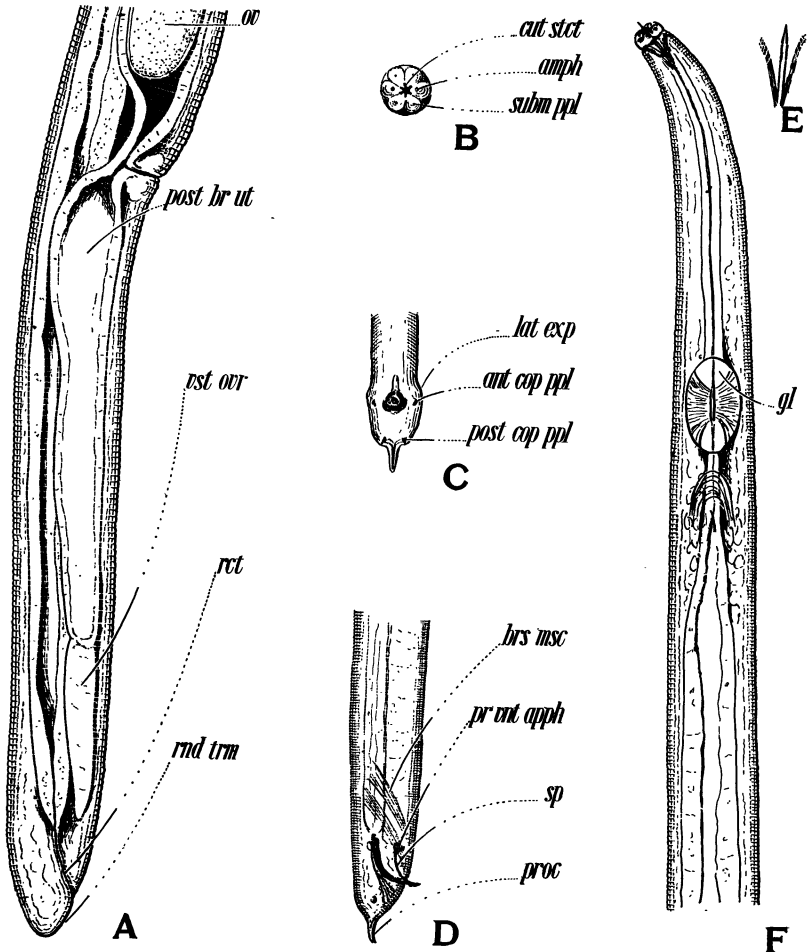


FIGURE 5.—*Aphelenchoides acroposthion*. A.—Posterior portion of female: *ov*, egg; *post br ut*, posterior branch of uterus; *vst ovr*, vestigial ovary; *rct*, rectum; *rnd trm*, rounded tail. \times about 720. B.—Front view of head: *cut stct*, cuticularized structure; *amph*, amphid; *subm ppl*, submedial papilla. \times about 940. C.—Tail of male, ventral view: *lat exp*, lateral expansion; *ant cop ppl*, anterior copulatory papilla; *post cop ppl*, posterior copulatory papilla. \times about 720. D.—Tail of male, lateral view: *hrs msc*, bursal muscles; *pr vnt apph*, process of ventral apophysis; *sp*, spiculum; *proc*, hornlike process (mucro.). \times about 720. E.—Free-hand sketch of spear. F.—Anterior portion of body: *gl*, granulated portion of esophageal bulb. \times about 720

nemas are considered (free association, carrier relationship, ectoparasites, endoparasites). The taxonomy of the genus *Aphelenchoides* and three nemas new to science, *Diplogaster occidentalis*, *Aphelenchoides conurus*, and *A. acroposthion*, are discussed and morphological descriptions given.